Postactivation potentiation in a human muscle: effect on the load-velocity relation of tetanic and voluntary shortening contractions

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Submitted 14 April 2007; accepted in final form 16 July 2007

Baudry S, Duchateau J. Postactivation potentiation in a human muscle: effect on the load-velocity relation of tetanic and voluntary shortening contractions. J Appl Physiol 103: 1318–1325, 2007. First published July 19, 2007; doi:10.1152/japplphysiol.00403.2007.—Recently it was demonstrated that postactivation potentiation (PAP), which refers to the enhancement of the muscle twitch torque as a result of a prior conditioning contraction, increased the maximal rate of torque development of tetanic and voluntary isometric contractions (3). In this study, we investigated the effects of PAP and its decay over time on the load-velocity relation. To that purpose, angular velocity of thumb adduction in response to a single electrical stimulus (twitch), a high-frequency train of 15 pulses at 250 Hz (HFT250), and during ballistic voluntary shortening contractions, performed against loads ranging from 10 to 50% of the maximum torque, were recorded before and after a conditioning 6-s maximal voluntary contraction (MVC). The results showed an increase of the peak angular velocity for the different loads tested after the conditioning MVC (P < 0.001), but the effect was greatest for the twitch (~182%) compared with the HFT250 or voluntary contractions (~14% for both contraction types). The maximal potentiation occurred immediately following the conditioning MVC for the twitch, whereas it was reached 1 min later for the tetanic and ballistic voluntary contractions. At that time, the load-velocity relation was significantly shifted upward, and the maximal power of the muscle was increased (~13%; P < 0.001). Furthermore, the results also indicated that the effect of PAP on shortening contractions was not related to the modality of muscle activation. In conclusion, the findings suggest a functional significance of PAP in human movements by improving muscle performance of voluntary dynamic contractions.

IN A RECENT STUDY (3), we demonstrated that postactivation potentiation (PAP), which refers to the enhancement of the muscle twitch torque resulting from a prior conditioning contraction (21, 26, 36, 40), increased the maximal rate of torque development of isometric tetanic (15 pulses, 250 Hz) and voluntary ballistic contractions to a similar extent. We also observed that the maximal potentiation of the rate of torque development was reached 1 min after the conditioning contraction, although twitch PAP was maximal immediately following the conditioning contraction. These results indicate that PAP can enhance the maximal rate of torque development of voluntary isometric contractions, but the significance of PAP during shortening contractions remains undefined. The lack of convincing data led Sale (36) to speculate in a recent review that PAP would have a greater effect for shortening compared with isometric contractions based on the rightward shift of the force-frequency relation in the former condition. Indeed, for a given frequency of stimulation, the torque produced during shortening contractions is lower than that observed in isometric contractions (6). As PAP exhibits a greater effect at submaximal forces compared with maximal or near-maximal forces (1, 30, 32, 40), shortening contractions would be more sensitive to PAP compared with isometric contractions.

Very few studies have directly investigated the influence of PAP on muscle performance during shortening contractions. Among these studies, Grange and coworkers (19) showed an enhancement of the maximal shortening velocity (~10%) and an upward shift of the force-velocity relation following a 5-Hz, 20-s stimulated conditioning contraction in mouse fast muscle. In humans, several performance studies have reported an increase in vertical jump height following a conditioning contraction (14, 17, 20, 42), an observation that suggests an increase in muscle power. However, none of these investigations measured the level of twitch potentiation, which is the most common tool to assess the presence of PAP. The latter point is important because Gossen and Sale (18) failed to demonstrate a PAP effect on the torque-velocity relation in the quadriceps muscle although the muscle twitch was significantly potentiated. Such divergent results bring into question the functional significance of PAP during dynamic contractions in humans. However, a difference in the rate of muscle activation during voluntary and electrically induced contractions might explain the difference between data obtained in isolated mouse preparation (19) and that obtained in human voluntary contractions (18). Indeed, it has been shown that the degree of potentiation is influenced by the frequency of stimulation (29) likely because the effect of PAP on the contractile kinetics depends on how the successive mechanical responses summate during repetitive activation (4).

Therefore, the main purpose of this study was to investigate the effects of PAP and its decay over time on the load-velocity relation in the human thumb adductor muscles. To examine whether PAP-induced changes in the performance measures of shortening contractions are related to the modality of muscle activation and to determine the locus of potentiation (muscular vs. nervous system), we compared voluntary and electrically induced contractions. An investigation on the potential benefit from PAP during voluntary contractions is relevant because most activities in sport, as well as activities of daily living, involve dynamic contractions.
MATERIALS AND METHODS

After informed consent was obtained, experiments were conducted on 10 subjects (3 women and 7 men) aged between 24 and 40 yr (28.3 ± 4.7 yr; mean ± SD). None of them presented any signs of neurological disorders. Subjects were all right-handed and instructed to refrain from heavy arm exercise 24 h before testing. They attended the laboratory on two occasions: one session consisted of testing the effect of PAP on the load-velocity relation from electrically induced contractions; a second session assessed the effect of PAP on the load-velocity relation under voluntary contractions. The experimental procedure was approved by the local Ethics Committee and performed in accordance with the Helsinki Declaration.

Experimental Apparatus

The subject was seated in a comfortable armchair to keep the shoulder and arm relaxed throughout the experiment. The right hand was placed horizontally and secured in a prone position by means of a custom-made apparatus (Fig. 1). The thumb was maintained in full extension, in the same plane as the palm, by a splint that prevented movement at the phalangeal joints of the thumb. The hand was positioned so the axis of rotation of the metacarpophalangeal joint of the thumb was aligned with the splint’s axis of rotation. To measure the torque produced during both maximal isometric tetanic and voluntary contractions, the splint was connected to a force transducer [sensitivity, 0.27 V/N·m; linear range, 0–15 N·m] via a removable steel rod (Fig. 1). A potentiometer (sensitivity, 1 V/ rad) was connected to the splint’s axis of rotation to measure angular displacement of the thumb. Inertial loads were attached to the splint via an inextensible steel cable during the shortening contractions. All movements started from a thumb angle of 0.87 rad (full adduction: 0 rad). This angle corresponds to the optimum thumb angle for maximal adduction torque (8). Because full adduction of the thumb was not possible with our setup, the total range of angular displacement was 0.35 rad.

EMG Recordings

The surface EMG from the adductor pollicis muscle was recorded by means of two silver disk electrodes (8-mm diameter) separated by 1 cm and placed over the muscle belly. The ground electrode was located on the pisiform bone, between the stimulating and EMG recording electrodes. The EMG signal was amplified (×1,000) and filtered (10 Hz-1 kHz; common mode rejection rate: 115 dB) by a custom-made differential amplifier. The torque and the EMG signals were recorded on a computer, at a sampling rate of 2 kHz, and analyzed off-line by using the AcqKnowledge data analysis software (model MP150; Biopac System, Santa Barbara, CA).

Stimulation Procedure

The adductor pollicis muscle was stimulated by rectangular electrical pulses (0.5-ms duration) delivered through two electrodes (silver disks, 8-mm diameter), placed over the ulnar nerve at the wrist. A digital timer (Master-8, AMPI, Jerusalem, Israel) was used to trigger the stimulator (Grass S88K, Astra-Med, West Warwick, RI). Maximal electrical stimulation was determined by progressively increasing the intensity until the compound muscle action potential (M-wave) and the mechanical twitch reached their maximal value. The level of stimulation for the protocol was set at ~20% above maximum.

Experimental Procedure

Protocol 1: high-frequency train of stimuli. High-frequency stimulus trains of 15 pulses delivered at a frequency of 250 Hz (HFT250) were used to induce contractions that reached the maximal rate of torque development in the adductor pollicis muscle (3, 9, 31). Because the HFT250 did not evoke a maximal tetanic torque plateau and consequently did not allow the recording of the maximal tetanic torque (3), the experiment began with the recording of three tetanic contractions consisting of 50 pulses at a frequency of 100 Hz (HFT100; 0.5-s duration) separated by 2-min intervals. The largest response was taken as the maximal tetanic torque (Tmax) and served to calculate the loads used in the successive protocols: 10, 20, 30, 40, and 50% of Tmax. Following the tetanic contractions, subjects rested during the placement of the recording electrodes. This period lasted ~20 min, which was sufficient to abolish any potentiating effect induced by the previous contractions (2, 4, 26, 40). Subjects then performed the five protocols in random order at the five previously reported loads. Before performing the conditioning maximal voluntary contraction (MVC), the responses to three single twitches (twitchbefore) and one HFT250 followed after 5 s by one single twitch (twitchafter; Fig. 2A) were recorded. These responses were obtained under shortening contractions. The twitchafter was used to probe the possible potentiating effect of the HFT250 on the twitch. Thereafter, subjects performed a 6-s conditioning MVC. The tests carried out during the recovery period consisted of one twitchbefore, one HFT250, and one twitchafter delivered in the following sequence: 5 s after the conditioning MVC; every minute until 5 min; and after 10 min (Fig. 2A). A minimum of 10 min rest period was provided to ensure that twitch parameters recovered their control value before the beginning of the next load protocol. In addition, after the 10-min rest period, three twitches were elicited, and the subsequent protocol began only if twitch amplitude did not differ by more than 5% from the initial control values.

Protocol 2: voluntary contractions. The experiment began with the recording of three MVCs (3- to 4-s duration) separated by 2-min intervals. The largest response was taken as the maximal voluntary
torque (Tvmax) and served to calculate the loads used in the successive protocols: 10, 20, 30, 40, and 50% of Tvmax. For ~10 min, subjects performed ballistic contractions (the subject was instructed to cover the entire range of displacement as fast as possible) against the five loads mentioned above. Subjects performed several sets of 5–15 contractions (the number of contractions being reduced when the load increased) to familiarize themselves with the procedure. To minimize any possible fatigue effect induced by the familiarization procedure, subjects rested for 3–5 s between contractions, with each set separated by 1 min of rest. After the familiarization program, subjects rested during the placement of the stimulating and recording electrodes (~20 min). Subjects then performed the five protocols in random order at the five previously reported loads. The testing protocol began with the recording of three twitches (twitchbefore), then five ballistic voluntary contractions, each separated by 1–2 s, followed 5 s later by a single twitch (twitchafter; Fig. 2B). After these control recordings, subjects performed the 6-s conditioning MVC, followed by one twitchbefore, five ballistic contractions, and one twitchafter. The different tests during the recovery period were carried out with the same timing used for the high-frequency train protocol (Fig. 2B). The procedure described for protocol 1 was used to ensure that twitch parameters recovered their control value before the beginning of the next load protocol.

**Measurements**

**Electrically induced contractions.** The average torque developed in response to the HFT100 (Tmax) was measured during 0.3 s once the torque plateau was reached. For all movements, the peak angular displacement of the thumb during single stimulus (twitch) or train of stimuli (HFT250) was measured. The angular velocities were also obtained from the first derivative of the displacement signal using the following formula: ṙ = (Finput(n + (m/2)) − Finput(n − (m+1)/2))/dt, where m is the number of intervals difference, n is the sample number, and dt is the time sampling interval. The signal was then smoothed by means of a moving average window of 20 data points. The PAP effects on the twitch and HFT250 were measured and expressed as a percentage of the twitch before. The potentiating effect of the five ballistic contractions on the twitchafter were expressed as a percentage of the twitch before. The peak-to-peak amplitude of the M-wave was measured from the EMG signal in response to a single stimulus. The control values for the M-wave and the twitchbefore were computed from the average of the three responses.

**Voluntary contractions.** The average torque value (Tvmax) during the MVCs and the associated averaged (rectified) EMG (aEMG) were measured during a 1-s epoch at the torque plateau. The angular displacements during the shortening contractions were measured, and angular velocities were computed the same as the electrically induced contractions. The PAP effects on the twitch and ballistic contractions were expressed as a percentage of the control values recorded before the 6-s MVC, and the potentiating effect of the five ballistic contractions on the twitchafter were expressed as a percentage of the twitch elicited before (twitchbefore) the ballistic contractions. The aEMG activity was analyzed from its onset to the time at which the peak angular velocity was reached.

**Load-velocity relation.** To compare the potentiation effect on angular velocity for tetanic and ballistic contractions, the load-velocity relations were determined. For each subject, the peak angular velocity (ω; rad/s) of each thumb displacement was plotted against the associated load (expressed as a percentage of Tmax or Tvmax). The data from both protocols were then fitted by a rectangular hyperbola based on Hill’s equation, (T + a)(ω + b) = b(ωmax + a) = constant, where T is load expressed as a percentage of Tmax or Tvmax, ω is angular velocity, Tmax is maximal isometric torque (Tmax or Tvmax is for tetanic or ballistic contractions, respectively), and a and b are constants (24). Maximal angular velocity (ωmax) at zero load was calculated theoretically for each subject from the experimental data, using the linear representation of Hill’s equation: (Tmax − T)/ω = T/ωmax + alb. The Tma ratio, which is an index of the curvature of the relation, was also calculated. The power curve (expressed in W) was determined from the following equation: b · T(Tmax − T)/(T + a). The peak power, which is known to occur at a fraction of the maximal isometric tension, was computed from the following expression: a/(ωmax/a + 1 − 1).

**Fig. 2.** Schematic representation of the 2 main protocols: high-frequency train of stimuli (A) and ballistic contractions (B). Twitchbefore and twitchafter are the mechanical responses to a single maximal electrical stimulus before and after a short high-frequency (250 Hz) train of electrical stimuli (HFT250) or 5 ballistic voluntary contractions, respectively; 6-s MVC corresponds to a 6-s conditioning maximal voluntary contraction.
Statistics

In control conditions, angular displacements and angular velocities of the thumb during the twitch$_{before}$, as well as the potentiating effect of the HFT$_{250}$ and ballistic contractions on the twitch$_{after}$, were compared between protocols and loads by means of a two-way ANOVA with repeated measures (protocol $\times$ load). Absolute values for peak power, the load at which the peak power was reached and $a/T_{\text{max}}$ from HFT$_{250}$, and voluntary load-velocity relations before the conditioning MVC were compared between protocols by means of a Student’s paired t-test. The effects of the 6-s conditioning MVC on the angular displacement and angular velocity were analyzed by means of a three-way ANOVA (protocol $\times$ load $\times$ time) with repeated measures. The time course of change in peak power, fraction at which the peak power was reached and $a/T_{\text{max}}$ ratio from HFT$_{250}$, and voluntary load-velocity relations following the 6-s MVC were analyzed by means of a two-way ANOVA with repeated measures (protocol $\times$ time). When a significant main effect was found from ANOVAs, a Tukey post hoc test was used to identify the significant differences among the selected means. For all comparisons, the level of statistical significance was set at $P < 0.05$. Data are reported as means $\pm$ SD within the text and displayed as means $\pm$ SE in Figs. 3–6.

RESULTS

Reproducibility of the Conditioning MVC

During the various experimental protocols, each subject performed a total of 10 conditioning MVCs. MVC torque and associated aEMG did not differ from trial to trial ($P = 0.62$ and 0.73, respectively); accordingly, the data were collapsed across contractions. The average MVC torque produced by the thumb adductor muscles was $8.2 \pm 1.7$ N·m.

PAP and Muscle Twitch

The angular displacement induced by the twitch in control conditions decreased with an increase in the load (load main effect, $P < 0.001$). The displacement was small for the 50% of $T_{\text{max}}$ load ($2.7 \pm 0.8\%$ of the entire range of movement) compared with the displacement of the 10% load ($15.1 \pm 5.7\%$). Therefore, the analysis of twitch PAP was focused on the twitch produced against the 10% load ($15.1 \pm 5.7\%$). Therefore, the analysis of twitch PAP was focused on the twitch produced against the 10% load. There was no significant difference between the two protocols for peak angular velocity before the conditioning contraction (Student’s t-test, $P = 0.14$); therefore, the data were collapsed across the two protocols. The average peak angular velocity of the twitch was $0.64 \pm 0.60$ rad/s. Similarly, following the 6-s MVC, the angular velocity between protocols was not significantly different; however, the collapsed values for the angular velocity of the twitch reached $281.6 \pm 46.7\%$ of the control value and were significantly potentiated (Tukey post hoc test, $P < 0.001$). The effect of PAP was maximal immediately following the conditioning contraction but declined rapidly during the first minute of the recovery period and then more slowly, finally returning to control values within 10 min (Fig. 3). In contrast, the M-wave peak-to-peak amplitude was not affected by the conditioning MVC (collapsed values for control and 5 s after the MVC: $4.7 \pm 2.9$ and $4.9 \pm 3.1$ mV, respectively; $P > 0.05$).

The muscle twitch (twitch$_{after}$) that followed each HFT$_{250}$ trial and set of five ballistic contractions was also influenced by the conditioning MVC (protocol $\times$ time, $P < 0.001$). In the control conditions, the peak angular velocity of the twitch$_{after}$ reached $127.7 \pm 22.2\%$ of the twitch$_{before}$ following HFT$_{250}$ (Tukey post hoc test, $P < 0.001$) and $159.2 \pm 24.1\%$ of the twitch$_{before}$ following the five ballistic contractions (Tukey post hoc test, $P < 0.001$). The data between the two protocols differed significantly (Tukey post hoc test, $P < 0.001$). Immediately after the 6-s conditioning MVC, the twitch$_{after}$ following the HFT$_{250}$ and ballistic contractions dropped similarly to 96.3 $\pm 13.1\%$ and 94.7 $\pm 13.7\%$ of the twitch$_{before}$, respectively (Tukey post hoc test, $P < 0.001$). However, the effect of HFT$_{250}$ on twitch$_{after}$ returned to the control value (Tukey post hoc test; $P = 0.86$) within 1 min after the conditioning MVC, whereas the effect of the five voluntary ballistic contractions remained reduced until the third minute of the recovery period (Tukey post hoc test, $P < 0.01$).

Load-Velocity Relation

There was a load $\times$ time interaction after the conditioning MVC ($P < 0.001$) although the two protocols did not differ (protocol $\times$ load $\times$ time, $P = 0.77$), so the data were collapsed across protocols. Regardless of the load, the maximal potentiating of the angular velocity occurred 1 min after the conditioning MVC (Tukey post hoc test, $P < 0.001$). The peak angular velocities reached $114.3 \pm 5.6\%$, $113.8 \pm 4.8\%$, $113.4 \pm 4.6\%$, $113.2 \pm 4.5\%$, and $113.8 \pm 4.5\%$ of the control values for loads of 10, 20, 30, 40, and 50%, respectively (Fig. 4). The angular velocity for the load of 10% MVC was potentiated for a duration of 5 min following the 6-s MVC (Tukey post hoc test, $P < 0.01$), whereas for heavier loads, it was only increased from the first to the fourth minute following the conditioning contraction (Tukey post hoc test, $P < 0.01$). In contrast, the aEMG during ballistic contractions was not changed throughout the recovery period (load $\times$ time, $P = 0.52$).

Before the conditioning MVC, peak angular displacement during the tetanic contraction (HFT$_{250}$) was reduced (ANOVA, $P < 0.001$) with an increase in load and reached $0.35 \pm 0.01$, $0.29 \pm 0.03$, $0.22 \pm 0.08$, $0.13 \pm 0.05$, and $0.13 \pm 0.05$ rad for loads of 10, 20, 30, 40, and 50%, respectively. The angular displacement was increased for loads of 30, 40, and 50% MVC (load $\times$ time, $P < 0.001$) between the first and third minute following the 6-s MVC (Tukey post hoc test, $P < 0.05$) with the greatest effect observed at 1 min.

The load-angular velocity relations illustrated in Fig. 5 were fitted by a rectangular hyperbola for the HFT$_{250}$ (Fig. 5A) and
 voluntary contractions (Fig. 5B), before and 1 min after the conditioning MVC. Before the conditioning MVC, the \( aT_{\text{max}} \) ratio was significantly lower for tetanic contractions (0.13 ± 0.1) compared with voluntary contractions (0.52 ± 0.3; Student’s \( t \)-test, \( P < 0.01 \)). Consequently, the peak power developed under tetanic contractions (4.0 ± 1.6 W) was lower than under voluntary contractions (8.8 ± 4.1 W; Student’s \( t \)-test, \( P < 0.01 \)). Furthermore, the load at which the peak power was obtained represented a lower percentage of the maximum torque (26.6 ± 8.7 % of \( T_{\text{max}} \)) under tetanic contractions compared with voluntary contractions (36.7 ± 4.2% of \( T_{\text{vmax}} \); Student’s \( t \)-test, \( P < 0.05 \)).

There was a significant time main effect (\( P < 0.001 \)) for peak power after the conditioning MVC, although no protocol \( \times \) time interaction was noted (\( P = 0.45 \)). Therefore, the data from the two protocols were collapsed. Peak power was potentiated from the first to fifth minute following the conditioning MVC (Tukey post hoc test, \( P < 0.001 \)) with a maximal change (113.4 ± 4.3% of the control value) observed 1 min after the conditioning MVC (Fig. 6B). In contrast to the enhancement of the peak power, neither the fraction of the maximal isometric torque at which the peak power was obtained nor \( aT_{\text{max}} \) ratio were significantly changed after the 6-s MVC (protocol \( \times \) load \( \times \) time; \( P = 0.99 \) and \( P = 0.89 \), respectively).

When \( \omega_{\text{max}} \) was calculated theoretically from the experimental data using the linear representation of Hill’s equation, \( \omega_{\text{max}} \) differed (Student’s \( t \)-test, \( P < 0.05 \)) between HFT\( _{250} \) (10.6 ± 3.8 rad/s) and voluntary contractions (8.0 ± 3.0 rad/s). Following the conditioning MVC, there was a significant time main effect (\( P < 0.001 \)) for \( \omega_{\text{max}} \), although no protocol \( \times \) time interaction was noted (\( P = 0.29 \)). After collapsing the data from the two protocols, \( \omega_{\text{max}} \) was found to be significantly potentiated during the first 5 min of the recovery period (Tukey post hoc test, \( P < 0.01 \)) with the greatest effect observed at 1 min (Tukey post hoc test, \( P < 0.001 \); Fig. 6A).

**Discussion**

This study was designed to investigate the effect of PAP on the load-velocity relations under electrically induced and ballistic voluntary contractions in the thumb adductor muscles. Our results show that 1) the increase in peak angular velocity was larger for a single stimulus (twitch: ~182%) compared with a high-frequency train (HFT\( _{250} \)) or ballistic voluntary contractions (~14%); 2) potentiation was maximal for the twitch immediately following the conditioning MVC but was delayed to 1 min for HFT\( _{250} \) and ballistic contractions; 3) twitch potentiation declined nearly exponentially over time returning to baseline within 10 min of recovery, although the angular velocity for HFT\( _{250} \) and ballistic contractions declined.
computed from the following expression:

\[ \text{Tmax} = \frac{\text{Tmax}_0}{a} \left( 1 - \frac{1}{1 + r} \right) \]

where \( \text{Tmax}_0 \) is the maximum isometric torque. *Significant difference (\( P < 0.05 \)) from control values. All data are expressed as means ± SE for 10 subjects.

more progressively until 4–5 min after the conditioning MVC. Although relatively small compared with the twitch, the similar potentiation of the angular velocity for tetanic (HFT250) and voluntary contractions indicates that PAP is not specific to the modality of muscle activation. These results, combined with those reporting a potentiation of the maximal rate of isometric torque development after a conditioning contraction in the thumb adductor muscles (3), emphasize the functional role of PAP during fast voluntary contractions of different types.

**Technical Considerations**

Classically, the force-velocity relation is computed from isotonic or isokinetic shortening contractions that follow a maximal activation of the muscle at constant muscle length. In the present study, we chose to measure muscle performance through the speed of moving joints against different inertial loads as is the case in natural movements. This was done for two reasons: 1) it is difficult to ensure constant force or speed of shortening of the contractile component in human muscles in situ because of changes in the lever arm during angular displacement; and 2) to quantify the effect of potentiation on muscle performance, it is necessary to keep the muscle at rest before the shortening contraction to avoid the confounding effect of the preactivation with the conditioning 6-s MVC. Therefore, our data cannot be directly compared with those derived from the classical force-velocity relation. First, the force produced by the muscle is not equivalent to the mass of the inertial load attached to the thumb because it is accelerated throughout the movement. Second, the speed of shortening was not kept constant during displacement, and the force did not reach a steady state as is the case in animal preparation (6). Third, muscle was not maximally activated at the beginning of the shortening phase, and consequently, the shape of the load-velocity curve can be influenced by changes in the contribution of the series elastic component (9). Indeed, even if the initial length was kept constant in our setup, the contractile component would have first taken up the slack of the series elastic component before the displacement could take place, a condition that differs as a function of the load (9). Despite these methodological differences, we use Hill’s equation to fit our data and to extrapolate the \( \text{θ}_\text{max} \). In fact, we tested different fitting procedures, but each individual load-velocity curve was best fitted (\( r^2 > 0.96 \)) by Hill’s equation. Although the comparison of our data with the traditional force-velocity curve and associated extrapolations need to be made with care, the conclusions regarding the potentiation of the muscular performance cannot be influenced by the procedure used in the present investigation.

**PAP and Muscle Twitch**

To our knowledge, this is the first time that PAP effect on the muscle twitch was recorded under shortening contractions in humans. The results indicate that an increase in peak angular velocity of the twitch before against a load of 10% of \( \text{Tmax} \) was similar to that reported for the isometric rate of torque development in the same muscle following a 6-s conditioning MVC (3). Such twitch enhancement is in agreement with data from mouse fast muscle where twitch potentiation was associated with myosin light chain phosphorylation (19), the most likely mechanism for PAP (30, 43). Another factor that may have influenced the degree of potentiation is a change in the compliance of the series elastic component after the conditioning contraction. However, it has been reported that transient muscle contractions increase the compliance of tendon structures (27), a factor that would decrease rather than increase the extent of potentiation. Consequently, the observation of an unchanged M-wave peak-to-peak amplitude during PAP and a comparable potentiation for tetanic and voluntary contractions support the concept that PAP is mainly related to intramuscular mechanisms.

As observed in our previous study (3), the present results show that the size of the twitch after was increased by HFT250 and voluntary contractions. The degree of twitch potentiation observed after only five ballistic shortening contractions performed at intensities as low as 10% of \( \text{Tvmax} \) is comparable to the twitch enhancement following isometric ballistic contractions of only 20% of MVC torque (3). At first, these results could be surprising because little or no potentiation was reported after a sustained submaximal contraction (<75% MVC) of short duration (41). However, twitch potentiation observed in the present study after fast contractions against small loads could be related to a difference in involvement of motor units. It is indeed well established that a greater number of motor
units are recruited during fast voluntary contractions compared with sustained submaximal contractions performed at similar intensities (10, 13). Enhanced motor unit recruitment during fast contractions involves units with higher recruitment threshold (comprising faster-twitch muscle fibers) that display greater PAP capacity than motor units with lower recruitment thresholds (21). The potentiating effect of the test contractions (HFT250 and ballistic voluntary contractions) may explain why the twitch before did not follow a strict exponential decline during the recovery period in our study (Fig. 3), as is the case when PAP decay was tested by single twitches only (2, 4, 21, 37). Each HFT250 or set of five ballistic contractions contributed to a more sustained potentiation and probably influenced the normal PAP decay, with a greater effect induced by the five voluntary contractions.

Load-Velocity Relations During Voluntary and Electrically Induced Contractions

Before the 6-s conditioning MVC, load-velocity relations differed between electrically induced (HFT250) and voluntary contractions with a more pronounced curvature index ($a/T_{max}$) for the former compared with the latter (Fig. 5). Although the difference in the degree of curvature for the two activation conditions might have been overestimated by the fitting procedure, this observation is consistent with data from the literature. The load-velocity relation from electrically induced contractions usually exhibits a greater curvature in mammal (19, 35) and human muscles (7, 12) compared with load-velocity relations computed from voluntary contractions (see Fig. 5B; Refs. 5, 18, 22, 26, 33). This lower $a/T_{max}$ ratio for tetanic contractions is associated with a lower peak power compared with voluntary contractions.

The differences in maximal torque and in the shape of the load-velocity relation between tetanic and voluntary contractions may be explained by the fact that for electrical stimulation only the muscle that is innervated by the stimulated nerve trunk is activated, and thus in the electrical stimulation condition both parameters depend solely on the characteristics of the muscle that is stimulated. Among thenar muscles, only the adductor pollicis and the deep head of the flexor pollicis brevis are activated during stimulation of the ulnar nerve at the wrist. Other synergist muscles are activated during voluntary contractions and contribute to the maximal adduction force and shape of the load-velocity relation. Presumably, the optimal mechanical contribution of each of these muscles is obtained at different thumb angles (23), thereby linearizing the load-velocity relation. In addition, the relative distribution of fiber types within synergist muscles could influence the curvature of the load-velocity relation (15, 28, 38). Another difference between the two activation modalities is the significantly greater value of $c_{max}$ for the high-frequency train of stimuli compared with voluntary contractions. Such a difference might originate from greater motor unit synchronization and a faster discharge rate induced during HFT250 compared with ballistic contractions (10, 13, 22, 39).

Effects of PAP on the Load-Velocity Relation

The most important result of the present study is the potentiating effect of a 6-s MVC on the thumb angular velocity during voluntary shortening contraction for the different loads tested. Our results recorded in humans are consistent with a previous work in small mammal muscles reporting an increase in maximal velocity of shortening and an upward shift of the force-velocity relation (19). Importantly, as discussed previously in the literature (1, 3), these changes were observed without any enhancement of the maximal force capacity of the muscle recorded during maximal electrically induced and voluntary contractions.

In a relevant review, Sale (36) suggested that the effect of PAP should be greater in shortening compared with isometric contractions because of the rightward shift of the force-frequency relation (6) and a greater potentiating effect at submaximal force compared with maximal or near-maximal forces (30, 32, 40). Our results failed to confirm this assumption since the potentiation of the rate of torque development for tetanic contractions (HFT250) performed during shortening and isometric conditions was comparable (14% vs. 17%, respectively; Ref. 3). A similar potentiation (14% vs. 15%) was also observed for fast isometric and shortening voluntary contractions (3). However, the enhanced peak angular velocity for voluntary shortening contractions lasted until the fifth minute after the conditioning MVC, although it disappeared after 1–2 min for voluntary isometric contractions (3). Therefore, the expectation of a greater potentiating effect for voluntary shortening compared with isometric contractions (36) is not supported by our data, but the two types of contraction are characterized by a difference in PAP duration. Another interesting result of the present study was the increase of the mechanical power. The potentiation of muscle peak power was similar and followed a comparable timing to that observed for angular velocities. However, the load at which peak power occurred was not influenced by PAP for either protocol.

The maximal effect of PAP on HFT250 and ballistic contractions was delayed (~1 min) compared with the twitch, similar to what has been observed for isometric contractions (3). The delay could be related to a saturation process that limits the extent of potentiation on the summation of the successive responses within a train of electrical stimuli delivered immediately after a conditioning contraction (2, 4, 11). This ceiling effect, probably linked to the level of free Ca$^{2+}$ concentration in the cytosol of the muscle fiber during repetitive muscle activations (30), is progressively reduced during the recovery period (2, 4). Furthermore, the drop of PAP for the twitch$_{after}$ associated with a reduction in maximal torque during an MVC and tetanic contraction immediately after the conditioning contraction (3), suggests that fatigue likely contributed to limiting potentiation during repetitive muscle activation (16, 34).

In conclusion, the main finding of the present study is a significant and similar enhancement of the peak angular velocity of electrically induced and ballistic voluntary contractions of the thumb adductor muscles associated with twitch PAP. Consequently, the load-velocity relations from electrically induced and ballistic voluntary contractions are shifted upward, and maximal power is increased for ~5 min following the conditioning contraction, with the greatest effect observed at 1 min. The increase in muscle performance during voluntary shortening contractions, at a time the muscle twitch is potentiated, indicates a functional role of PAP in human movements during daily tasks and in explosive sports.
ACKNOWLEDGMENTS

We are particularly grateful to Z. Riley and M. Jesunathadas (Univ. of Colorado, Boulder) for helpful comments on a previous version of this manuscript.

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